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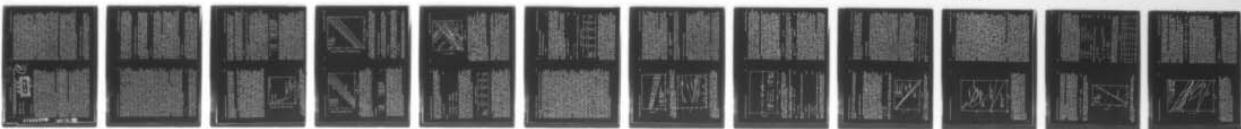
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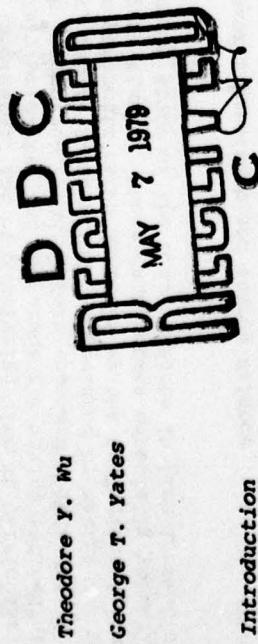
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III. A COMPARATIVE MECHANOPHYSIOLOGICAL STUDY OF FISH LOCOMOTION WITH IMPLICATIONS FOR TUNA-LIKE SWIMMING MODE



A. Introduction

In this highly valuable working conference on the physiological ecology of tunas, all factors involved in this general subject are examined. The scope, as elucidated in the preface by Magnusson, in the applications section by Sharp, and in the perspective discussion of the proceedings by Dizon and Sharp, is designed to promote a full interdisciplinary interaction between all the related fields. Thus, the subject matter is brought into a fine focus by the expository discussions given by the leading contributors on the cardiovascular function, respiration, metabolic rate, biochemistry and musculature, physiology, thermoregulation, hydrodynamics and energetics, all especially addressed to the tunas. The objectives are clearly aimed both at the scientific merit of advancing our knowledge in this specific field and at improving the techniques for practical application.

The study of tuna locomotion is not only of great interest to the fluiddynamicist, but has a pertinent interface with studies of the metabolism and energetics, feeding and migration, growth and spawning, and other behavioral and physiological properties of tunas that may depend on the environmental parameters. A better understanding of these interrelationships can illuminate the development of practical methods for optimum fishing strategies.

In hope of obtaining full benefit of multidisciplinary interactions with the distinguished participants and many others, we elect to discuss the hydrodynamic aspects of the tuna-like swimming mode by exploring what the biologist and the hydrodynamicist can accomplish with a close collaboration. If we combine the studies on thrust generation based on hydrodynamic principles of fish locomotion and those on metabolism and biochemical energy conversion, more useful data become available, thus reducing the number of unknowns necessary for our investigation. The joint approach often enables the selection of those data of direct interest that approach their value in nature. For example, the metabolic rate of a fish in self-propulsion can be measured in various cases to a high precision;

this is in sharp contrast to the formidable task of making direct flow measurements on the pressure and skin-friction distributions over the surface of a swimming fish. With further reference to the scaling effects (when the data cover a range of animal size), such joint studies often yield interesting relationships which would otherwise be difficult to achieve between the physiological and dynamical parameters. The profitable value of this approach to studies of animal locomotion has been well recognized, as demonstrated during the recent International Symposium on Scale Effects in Animal Locomotion (the Proceedings edited by Pedley, 1977). This further underlines the importance of close collaboration between scientists from different fields engaged in interdisciplinary research on topics such as the present one.

We shall therefore discuss scale effects in fish locomotion. Priority will be given to scaling problems of carangiform and lunate-tail locomotion of different groups of fishes, considering their hydrodynamic efficiency and physiological functions on the basis of data from both comparative zoology and dynamical similarity. The primary reason for choosing this rather broad area is because it is where experimental results are sufficiently abundant to allow refined investigations of the scaling problem. The present study is a further extension of the previous one by Wu (1977), now incorporating more recently available experimental data (on additional physical quantities). A modification of the analysis is introduced here by referring the metabolic rate to its basal state as datum so that the energy expended for maintaining a specified level of swimming activity is separated from the basal metabolism.

While specific application of this method to studies of scale effects in swimming of scombrid fishes certainly is desirable, it nevertheless requires new experimental results of metabolic rates at different activity levels together with further consideration of at least two features: (a) continuous use of pectoral fins for counterbalancing the negative buoyancy inherent to scombrids, which results in additional induced drag to forward motion; and (b) the presence of retial heat exchangers in their cardiovascular system, which may be a significant factor in their metabolism and should be taken into account for energetic evaluations.

B. Hydrodynamic Forces on a Swimming Fish

Swimming motions of large aquatic animals are characterized by large values of the ratio of typical inertial forces to typical viscous forces in the surrounding water, i.e., of the Reynolds number, $Re = Vl/\nu \gg 1$. Here V is the mean

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swimming speed, l the length of the animal, and v the coefficient of kinematic viscosity of the fluid. In general, the Reynolds number lies in the range $10^4 < Re < 10^8$ for various fishes and cetaceans swimming normally. At such high Reynolds numbers the effects of viscosity are mostly confined to a thin boundary layer adjacent to the body surface. This is especially true for the streamlined body shapes of such animals in undulatory swimming motion, when flow separation is not observed to occur, and only a very thin wake is formed behind the body. In such cases the boundary layer will continually grow with distance along the fish, but its maximum thickness (at the tail end) is generally not more than a few percent of the body thickness. Viscous effects can therefore be neglected in analyzing the flow outside this boundary layer. The pressures acting on the body are those predicted by inviscid theory because the boundary layer is too thin to support a pressure gradient across it. However, the viscosity of water is nonetheless responsible for shedding of vortex sheets from various fins of a swimming fish, which further modifies the pressure distribution of inviscid theory. These pressures (resulting from the inertial forces of water to the swimming motions of fish and from the interaction between body motion and shed vortex sheets) generate a thrust force which must overcome the drag force in order to maintain a constant forward velocity. The drag force in this case arises mainly from the viscous shear stresses exerted by the fluid on the body surfaces, which has a longitudinal and a transverse component at any body section. The contributions of "form drag" (resulting from the distal thickening of the boundary layer and possibly from flow separation) and of "wave resistance" (energy lost through making waves when swimming close to the water surface) are generally insignificant for these animals.

Thus the hydromechanical problem of fish locomotion can be conveniently divided into two parts: (a) thrust, determined from an analysis of the potential flow outside the boundary layer but involving the shed vortex sheets; and (b) drag of a swimming body, which in principle can be determined by calculating the viscous shear stress in the boundary layer or by direct measurement (Magnuson and Weininger, this volume). If the mean thrust is denoted by T , and the mean total drag by D , we have, in steady swimming,

$$(1) \quad T = D.$$

The mean thrust can be calculated quite accurately using the slender-body theory developed by Lighthill (1960, 1970, 1971), Wu (1971a), Newman and Wu (1973), and Newman (1973). In contrast, our knowledge, in both theoretical and experimental context, about the viscous resistance of a body in unsteady

motion in general, and of a swimming fish in particular, is still very primitive and too crude for making refined studies of fish locomotion by our modern standard. This deficiency, however, can be substantially alleviated by making use of the data on metabolic rates obtained by the biologists for a great variety of fishes. These data become especially valuable in the present study of the scale effects in fish locomotion.

C. Power Expenditure and Energy Balance

From the physical standpoint the minimum power necessary to transport the body at a given velocity V is determined by the resistance of the medium, the efficiency of the mode of locomotion, the energy consumption of the particular type of power plant that delivers the mechanical power, and many other factors. The principle of energy conservation may be expressed as

$$DV = \eta P, \quad (2)$$

which states that the animal's mean rate of working against the resistance D is provided by the power input P , used with efficiency η . For aquatic animals the variations of potential energy are generally unimportant, and in any case can be considered separately for the scombrids and other negatively buoyant fishes (Magnuson, 1973).

The power input for locomotion can also be determined by measuring the animal's metabolic rate and by applying standard energy conversion factors. Thus, when P in eq. (2) is taken to be the mechanical power, η is the hydrodynamic efficiency η_h of the propulsion. When P is taken instead to be the part of metabolic power used primarily for swimming (the rate at which biochemical energy is released as measured during a given level of active swimming minus the basal metabolic rate for maintaining normal resting functions), then η is equal to $\eta_h \eta_m$, where η_m is the efficiency with which biochemical energy is converted to muscle power.

D. Metabolic Rate

The extensive literature on the metabolism and swimming speeds of fish makes it plain that the physical details of an experiment must be clearly specified, in order that its results may be interpreted correctly. For example, see Winberg (1956), Drabkin (1959), and Brett (1965a,b). Of major importance in the study of the metabolic rate of a fish are its level of activity, its mass, and the temperature of the water. Such factors as preconditioning (a period of fasting and exercise

prior to the test, so that none of the fish's energy is spent in digesting or absorbing food during the test), the state of maturity and sex of the specimen, and flow conditions during the experiment are also important. We can give only a brief account here.

1. Level of activity. The level of activity in swimming fish is hard to characterize in general. However, for the salmon, a migratory fish, Brett (1965a,b, 1967a,b) found three levels of performance (see Fig. 1): sustained (speeds that can be maintained almost indefinitely), prolonged (speeds maintained for 1 or 2 hours with a steady effort, but leading to fatigue) and burst (speeds achieved at maximum effort lasting for only about 30 seconds). The physiological basis of each of these activity levels is different, and it itself depends on body size and environmental temperature. Apparently, the physiological parameters involved in characterizing different levels of activity are quite complex as they have been noted (Brett 1965a,b, for the salmon, and various other authors) to include such factors as preexercise, maturity, sex, varying use of red and white musculature, buildup of an oxygen debt and fatigue. Further, the metabolic process may vary with the kinematics of the bodily motion, which in turn may be modulated by the fluid reaction, and even the efficiency of energy conversion (Lighthill, 1973). For the Thunnini, an additional factor involves the biothermal heat-exchange mechanism, as previously discussed (Chapter 4, Thermal Biology of Tunas).

2. Scaling of the Metabolic Rate. The relationship between body mass and the metabolic rate of fish has received considerable attention, particularly for the resting state (for expository reviews see Kleiber, 1967; Schmidt-Nielsen, 1972b). The equation which describes this relationship is of the general form

$$P = am^b \quad (3)$$

where m is the body mass, and a and b are coefficients independent of body size.

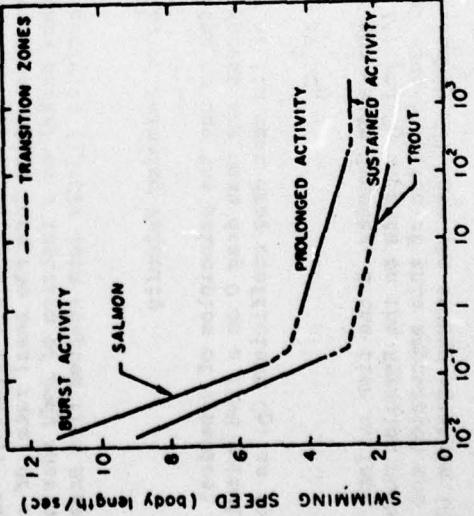
Various authors have considered body mass m directly. Winberg (1956) examined 266 cases for freshwater fish and obtained an average value of $b = 0.81$ (at 20°C). Heusner et al. (1963) investigated three species and derived an overall mean of $b = 0.73$ (at 25°C). There are other reports giving a rather wide range of values, varying all the way from near the "surface law" ($b = 0.67$) to direct total mass proportionality ($b = 1$).

Brett (1963, 1965a,b) has shed considerable and much-needed light on the problem by distinguishing between the different levels of activity. He provided the following results for sockeye salmon (*Oncorhynchus nerka*), with oxygen consumption measured in mg O₂ h⁻¹, and body mass in g (see also Fig. 2):

$$\begin{aligned} \log a &= -0.632 & b &= 0.775 \pm 0.145 \text{ (standard)} \\ &= -0.523 & &= 0.846 \pm 0.145 \text{ (1/4 max)} \\ &= -0.357 & &= 0.890 \pm 0.145 \text{ (1/2 max)} \\ &= -0.223 & &= 0.926 \pm 0.145 \text{ (3/4 max)} \\ &= -0.050 & &= 0.970 \pm 0.053 \text{ (max)} \end{aligned} \quad (4)$$

Here the fractions refer to the maximum speed which could be sustained for 60 min in fresh water at 15°C (V_{crit}), and his standard metabolic rate is obtained by extrapolating the O₂ consumption versus velocity curve to zero swimming velocity. In order to separate the metabolic power expended exclusively for propulsive purposes from the measured total metabolic rate, we propose, as a modification of the previous analysis of Wu (1977), which was based on direct adoption of (4) for the relationship (3), to extract the required information from Brett's experimental result by subtracting off the basal rate from the measured metabolic rates at different levels of activity for each specimen tested. This difference, which we shall assume to be the metabolic rate for swimming and which we shall denote again by P in the sequel, is plotted versus body mass in Fig. 3. With a least-square curve fitting, the intercepts and slopes of the regression lines are obtained

FIG. 1. Swimming endurance of sockeye salmon and rainbow trout. Transition zones between different levels of activity are shown with broken lines (after Brett, 1964, 1967b).



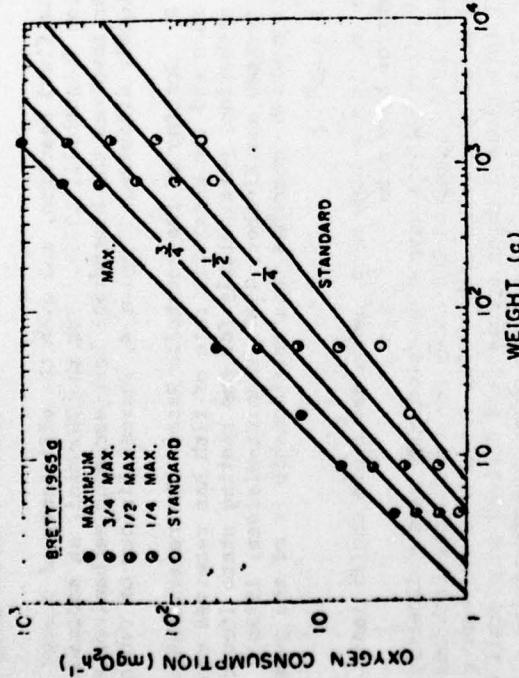


FIG. 2. Metabolic rate of sockeye salmon (*Oncorhynchus nerka*) as a function (see eq. 4) of body weight at various levels of swimming activity (15°C). The standard level was determined by extrapolation to zero swimming speed of the oxygen consumption versus speed relation. The full-activity line corresponds to the maximum speed which could be sustained for 60 min. V_{crit} . Intermediate fraction levels correspond to swimming speeds equal to 3/4, 1/2, and 1/4 of V_{crit} , respectively.

as follows:

$$\begin{aligned} a &= 0.103 & b &= 0.889 \text{ (1/4 max)} \\ &= 0.245 & &= 0.922 \text{ (1/2 max)} \\ &= 0.465 & &= 0.949 \text{ (3/4 max)} \\ &= 0.730 & &= 0.989 \text{ (max)} \end{aligned} \quad (5)$$

The primary advantage of using these derived data lies in the significance that the metabolic rate for swimming activities (in excess to its basal value) is now appropriately identified. A slight disadvantage, however, is some contamination of the highly accurate data at high levels of activity by the somewhat larger error contained in the basal-rate values as they were obtained by extrapolations in the first place. This contamination is quite likely worse for the data at lower levels of activity, and hence a word of caution is in order on any attempt to extrapolate the present results to very low activity levels below the 1/4 active.

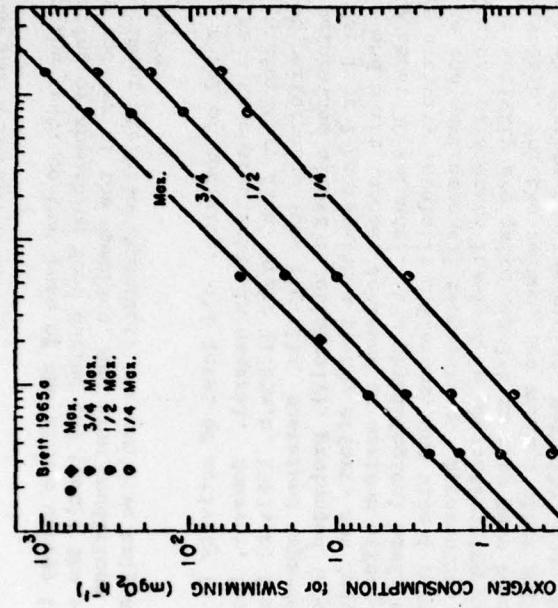


FIG. 3. The "metabolic rate for swimming," based on measured oxygen consumption less the basal rate, of sockeye salmon (*Oncorhynchus nerka*) as a function of body mass at various levels of activity (15°C); data adapted from Brett (1965a).

B. Scaling of Swimming Velocity

In order to use the principles of dynamical similarity, we first express the mean drag D on a fish swimming at speed v in terms of its mean drag coefficient C_D , as follows:

$$D = \frac{1}{2} \rho v^2 S C_D \quad (6)$$

where ρ is the water density, S the fish surface area (proportional to l^2), and C_D depends on the Reynolds number Re and the body shape. Substitution of this expression and the metabolic rate relationship (3) into the energy equation (2) then yields

$$v^3 \propto l^{3b-2}/C_D \quad (7)$$

Three limiting cases can be examined by assuming that for carangiform with lunate-tail swimming, in which case the fish

is well-streamlined, C_D is the same, apart from a shape factor, as that of a flat plate of the same area at the same Reynolds number. That is, C_D is proportional to $Re^{-1/2}$ or $Re^{-1/5}$ according to whether the boundary layer is laminar or turbulent. This leads to the scaling law:

$$V = \text{const. } t^{\beta} \quad (8)$$

with

$$\beta = \frac{3}{5} (2b - 1) \quad (\text{laminar})$$

$$\beta = \frac{3}{14} (5b - 3) \quad (\text{turbulent})$$

$$\beta = b - \frac{2}{3} \quad (C_D = \text{const.})$$

The last case (of quite large but constant C_D) corresponds to the situation for separated flow past a blunt body with a broad wake formation, or to the case in which flow separation occurs in the cross-flow past an undulating fish body. If the values for b given in (5) are adopted, we obtain Table I for β . The last column, for $b = 1$, is included to show the values of the index β when the metabolic rate is proportional to body weight, and the last row, for $C_D = \text{const.}$, is for the hypothetical case in which the flow is fully separated.

A collection of existing experimental data is given in Fig. 4. In the log V versus t plot for (a) Brett's 60-min maximum activity results for salmon at 15°C; (b) Beamish's (1966) results for 6 species of fish over a range of temperatures (8-14°C) and endurance spans; and (c) a few other sources (see Fig. 4 legend), the slope of the mean regression line is 0.5 (i.e., $\beta = 0.5$). This result led Brett (1965a,b) to propose "that the swimming speed is proportional to $t^{0.5}$, indicating a decrease in the relative ability to maintain a sustained speed as size increases." It is of interest to point out that the speed at the 1/4-max activity level ($b = 0.89$) of the sockeye salmon is also proportional to $t^{0.5}$ (see Fig. 4).

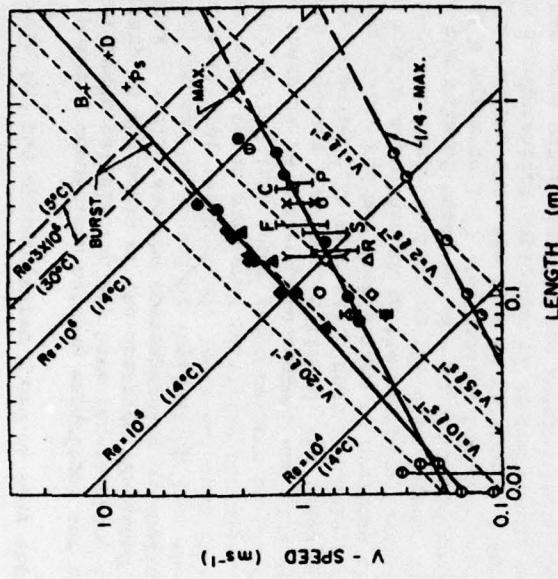


FIG. 4. Variation of swimming speed with body length at specific levels of activity. Burst speed data: ♦ dace, ▲ goldfish, ● trout, ▨ barracuda, P+ porpoise, Dt dolphin (Bainbridge, 1961); full activity data: open symbols (Bainbridge, 1961); ● sockeye salmon (15°C) (Brett, 1965a); ◊ bass, ● coho salmon (Dahlberg et al., 1968); C cod, R redfish, F winter flounder, S sculpin, P pout (Beamish, 1966); — goldfish (Smit et al., 1971); ◉ larval anchovy (Hunter, 1972); ✕ herring (Jones, 1963); ◊ salmon, ◊ trout (Paulick and Delacy, 1957). 1/4 - max data: ○ sockeye salmon at 15°C (Brett, 1965a). The lines of constant Reynolds number, Re, and lines of constant specific speed (in t^{-1} s $^{-1}$) are indicated for reference.

There are, however, other reports (Brett, 1967a; Magnuson, 1970; Hunter, 1971; Hunter and Zweifel, 1971) indicating that a better overall average value for β is 0.6.

Considerable attention has been given to the burst speeds which, for various species of streamlined fish, tend to be nearly independent of both size and temperature. A representative plot is included in Fig. 4, showing Bainbridge's (1961) results for 4 species of fish and two cetaceans; the slope of this line gives a value of β equal to 0.88. Similar values have been obtained by others, such as $\beta = 0.94$ for herring (at ~12°C) by Blaxter and Dickson (1959). In fact, a speed of 10 lengths per second has been regarded by several authors

TABLE I: Predicted β Values

b	β	$b = 0.89$	$b = 0.92$	$b = 0.95$	$b = 0.99$	$b = 1.00$
C_D	($\frac{1}{4}$ - max)	($\frac{1}{4}$ - max)	($\frac{1}{2}$ - max)	($\frac{3}{4}$ - max)	(max)	
laminar	0.47	0.50	0.54	0.59	0.60	
turbulent	0.31	0.34	0.38	0.42	0.43	
$C_D = \text{const.}$	0.22	0.25	0.28	0.32	0.33	

as a common rule for the maximum burst speed of many streamlined fish.

At this point a comparison between experiment and the foregoing similitude calculation may have far-reaching implications.

First, on the basis of the observed sustained speeds (with the index $\beta = 0.5$) and the corresponding metabolic-rate index $b = 0.99$, it may be argued by implication (see the fourth column of Table I) that the boundary layer adjacent to the swimming fish would be at most only partially turbulent up to Reynolds number of 10^6 (the upper range covered by the data). Furthermore, there is no evidence to suggest any flow separation. If this argument can be established, the study of the metabolism of swimming fish will yield most valuable results for hydrodynamicists, and may enable them to overcome the difficulties in making measurements in the boundary layer over an undulating body and hence estimating the drag force. Further, we note that the rule of burst-speed = $10t^{1/2}$ would correspond to a value of b equal to 1.33 (for laminar boundary layers), and even higher values when the flow is turbulent. Whether this implies a substantial depletion of stored energy or whether it has some other significance remains to be explored.

Similar dimensional analysis of the velocity-length scaling cannot as yet be carried out for the scombrids because no systematic measurements have been made of the metabolic rate at different specific levels of sustained cruising speeds.

Such experiments with an attempt to determine their basal metabolic rate (if meaningful at all) would be further complicated by their commitment to continuous swimming with a speed no less than their minimum cruising speed for maintaining lift by the Pectoral Fins (Magnuson, 1970). Available literature indicates that *Bathyynus affinis* (37-42 cm) swims voluntarily at $1.3 - 3.2 \text{ ls}^{-1}$ (Magnuson, 1970; Cahn, 1972) and increases its speed when stimulated by food. Walters (1966) has recorded fish (40 cm) of this species of tuna feeding at speeds between 3.8 and 10 ls^{-1} and nonfeeding speeds over the range from $2.9 - 12.5 \text{ ls}^{-1}$. In general, many species of the Scombridae can cruise for long periods at speeds up to 3 ls^{-1} . *Thunnus thynnus*, the giant bluefin tuna, grows up to 3 m in length and migrates over thousands of nautical miles, but at lower specific speeds ($\text{in } \text{ls}^{-1}$) than other scombrids of smaller maturity sizes. One record reported by Mather (1962) indicates a transatlantic migration of two large bluefin tuna (2.5 and 2.8 m long) at an average speed no more than 0.3 ls^{-1} . Although no definite conclusion can be drawn, these results suggest that a trend similar to that shown in Fig. 4 may be expected also to hold for the scombrids.

F. Specific Energy Cost of Transport

The nondimensional quantity

$$\epsilon = P/mgV \quad (9)$$

where g is the acceleration of gravity, provides a useful measure of the relative merit of different propulsive systems, and is called the "specific energy cost" of transport (Wu, 1977). It has been used by von Kármán and Gabrielli (1950) to evaluate the comparative merits of 14 classes of transportation vehicle, and by Schmidt-Nielsen (1972a), Tucker (1970, 1975), and others for studies of comparative physiology.

The results obtained above for the scaling of metabolic rate and swimming velocity may now be used to evaluate the scaling of the specific energy cost. From (9), (3), and (8) we immediately deduce that

$$\epsilon = P/mgV = \text{const. } m^{-\gamma} \quad (10)$$

where

$$\gamma = 1 - b + \beta/3. \quad (11)$$

Using Table I we obtain for γ the results shown in Table II.

TABLE II: Predicted γ Values

b	0.99 ($\frac{1}{4}$ -max)	0.92 ($\frac{1}{2}$ -max)	0.95 ($\frac{3}{4}$ -max)	0.99 (max)	1.00
C_D					
Laminar	0.27	0.25	0.23	0.21	0.20
turbulent	0.21	0.19	0.18	0.15	0.14
$C_D = \text{const.}$	0.18	0.16	0.14	0.12	0.11
from Fig. 5	0.28	0.25	0.22	0.18	

Figure 5 presents the experimental data, derived from those given in Figs. 3 and 4, showing how the specific energy cost varies with body size for fish swimming at different levels of activity. The solid lines are regression lines, obtained by a least-square error fit, with their slopes, γ values, given in the last line of Table II. These values of γ and the observed mean of $\beta = 0.5$ are plotted against b (which may be regarded as a measure of the level of activity) in Fig. 6. Also shown are the similarity predictions of β and γ given by (8) (or Table I) and (11) (or Table II) for the three distinct reference states characterized by a laminar

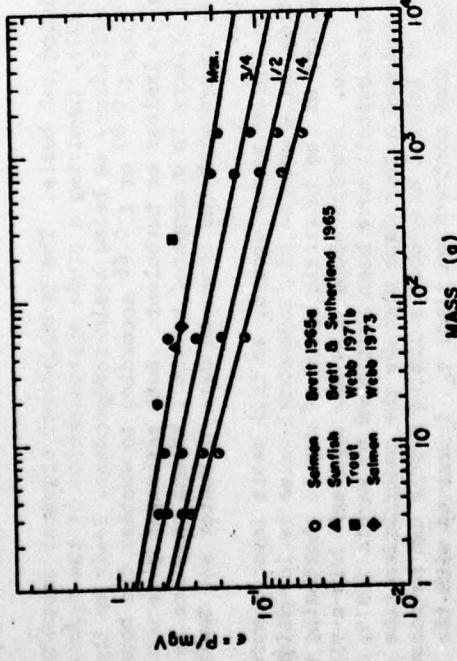


FIG. 5. Relation between specific energy cost for swimming, γ , and body mass for fish swimming at different levels of activity. Solid lines are regression lines obtained from data of Brett (1965a) for salmon at 15°C.

boundary layer, a turbulent boundary layer, and separated cross flow. The observed γ values agree well with the predicted laminar flow reference line and depart only slightly from it toward the turbulent flow state at higher activity levels. The observed mean of $\beta = 0.5$ also lies between these two reference states when the activity level is higher than the 1/2 maximum. These comparative results suggest that the boundary layers of these swimming fish would be at least partly laminar at the high Reynolds numbers tested ($10^4 < Re < 1.4 \times 10^6$) and with a distal part turbulent. We shall return to this point later in the discussion on viscous resistance.

The specific energy cost of transport has also been discussed in the recent studies of Schmidt-Nielsen (1972a) and Tucker (1975) for the locomotion of various animals. For comparison we find, from Schmidt-Nielsen's Figure 1a and Tucker's Figure 2, that their observed values of γ for fish are

$$\gamma = 0.30 \quad (\text{Schmidt-Nielsen}), \quad (12)$$

$$\gamma = 0.27 \quad (\text{Tucker}). \quad (13)$$

These values of γ are slightly greater than the present result (listed in the last row of Table III), and this difference could be caused by possible inclusion of the basal metabolic rate in their calculation.

C. Scaling of Tail Beat Frequency

Bainbridge (1958a, 1960, 1963) observed that the maximum amplitude of tail beat of fishes in carangiform motion is approximately 0.2 of the fish length l , with no noticeable dependence on other parameters. Further, the "reduced frequency," $\sigma = \omega l / N$, where ω is the radian frequency (thus the tail-beat frequency $f = \omega/2\pi$), is scale-independent at high levels of activity, and takes values around 1.0. Observations by other authors are essentially in agreement with Bainbridge's. According to the detailed analysis of Hunter and Zweifel (1971), the reduced frequency of jack mackerel was found to be constant in experiment only for values of f above some minimum tail-beat frequency. At high activity levels, σ lies between a mean value of 10 and 8. Similar results have been reported by Pyatetskii (1970a) for several fast fish species. These observations indicate that scaling of σ appears to be different at low activity levels.

Figure 7 shows a set of data on σ collected from various sources with the values at low activity levels excluded. In all the data exhibited there was no specific information about the activity level at which the frequencies were measured, and, possibly as a consequence, there is considerable scatter in the

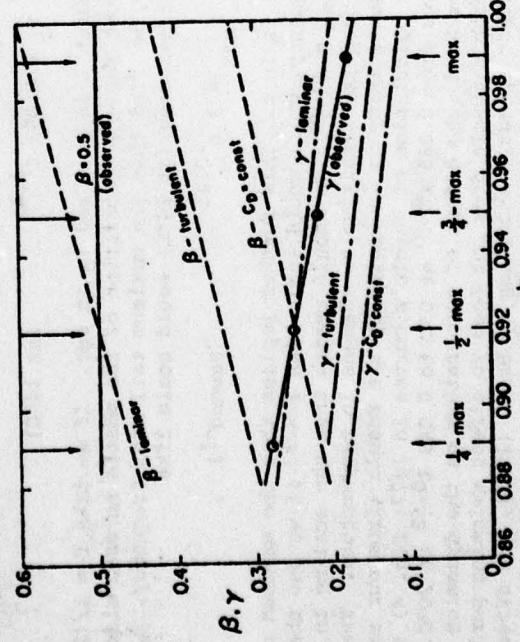


FIG. 6. Comparison of the observed values of β (Brett, 1965a,b) and γ (see Fig. 5 and Table II) with the similarity predictions (eqs. 9,11) based on the three distinct reference states characterized by a laminar boundary layer, a turbulent boundary layer, and $C_D = \text{const.}$ (for the case of separated cross flows).

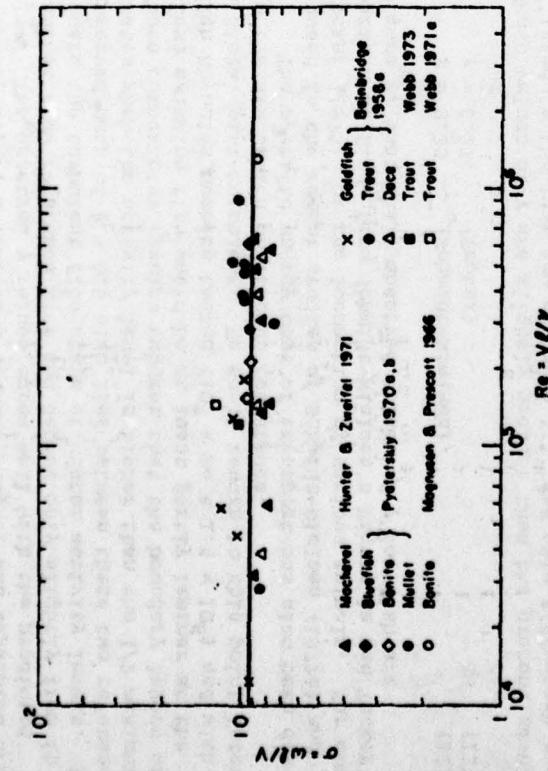


FIG. 7. Dependence of the reduced frequency, σ , on the Reynolds number, Re , for a variety of fishes. Only data for fish swimming near V_{crit} are presented. Solid line is a least-square error line fit to the data.

result. Nevertheless, a least-square error fitting yields that over the desired range of Reynolds number,

$$\sigma = \omega_0/V = 9.2 \quad \text{or} \quad \sigma = 9.2 \quad (14)$$

$$\text{and} \quad \sigma = 1.5 V/\ell_0 .$$

This result indicates that when combined with the velocity scaling,

$$V = K_V f^{0.5} , \quad (15)$$

f then scales like

$$f = K_f t^{-0.5} , \quad (16)$$

$$K_f = 1.5 K_V .$$

Here the coefficients K_V and K_f both depend on the activity level.

It would be illuminating if the simple relationship (14) showing the reduced frequency in swimming as being nearly scale-independent can be explained on a hydromechanical or

physiological basis. The hydrodynamic argument suggested by Wu (1977), involving a crude approximation of the hydromechanical efficiency as being scale-independent, leads to the scaling of f like $f^{-0.88}$ or $f^{-0.65}$ according to whether the boundary layer is laminar or turbulent. Both estimates give too strong scale effects in σ compared to (14), though they are in qualitative accord with the observed data of Hunter and Zeifel (1971).

On physiological ground, as tail beats involve muscle contraction, it should be of fundamental value to investigate variations of the intrinsic speed of muscle shortening with animal size. Studies along this new approach (vis-a-vis the phenomenological) have been initiated by Wardle (1975, 1977) who developed a technique whereby the contraction time of pieces of lateral anaerobic swimming muscle can be measured. He found that contraction time, τ_C , increased with the length L of the fish and with decrease in temperature (by 0.001 sec per 1°C). The minimum contraction time (hence with maximum beat frequency) at 14°C , derived from the regression line corresponding to Wardle's data and curve (1977: fig. 4), can be expressed as

$$\tau_C = 0.053 f^{0.45} \quad (\text{at } 14^\circ\text{C}) \quad (17)$$

in which f is in m s^{-1} and τ_C in sec. If we take $f = 1/(2r_C)$ to account for one contraction of the muscle on each side of the body, we find that the maximum tail-beat frequency, f_{max} , in burst swimming (at 14°C) would scale like

$$f_{max} = 9 f^{-0.45} \quad (\text{second}^{-1}) , \quad (18)$$

if f is in m s^{-1} . This further implies that the maximum reduced frequency, σ_{max} , would scale like $f^{-0.33}$ if we use the scaling $V_{burst} \propto f^{0.88}$. We should remark that the scaling in f_{max} may be quite sensitive to changes in temperature. The degree of sensitivity is indicated by the result (from our regression-line calculation of Wardle's curves in 1977: fig. 4) that r_C varies from 0.065 m at 0°C to 0.048 m at 20°C . On the other hand, the effect of temperature on the dynamics of anaerobic muscle does not seem to affect swimming performance at burst speeds. According to Brett (1963), the effect of temperature diminishes with increasing speed such that burst speeds become independent of temperature; this interesting phenomenon remains to be clarified.

This is another example, like studies on the relationship between size and metabolism, of how this subject can be illuminated by acquiring a basic understanding of the physiological mechanism underlying the phenomenon. Clarification of scale effects (or lack of them) in σ , given by (14), would benefit

from joint studies on dynamics of aerobic muscle at different activity levels of sustained swimming and the hydrodynamics involved.

H. Propulsive Body-Wave Speed

According to the slender-body theory for fish locomotion cited earlier, both the thrust and hydromechanical efficiency depend on the ratio, V/c , of the swimming speed, V , to the wave velocity, $c = f\lambda$, of the wave (of frequency f and wavelength λ) which is propagated along the body. It has been noted that positive thrust is associated with values of $c > V$ and high efficiencies correspond to small values of $(1 - V/c)$. Pyatetskiy (1970b) has further observed experimentally that the swimming speed V increases as the wave speed c decreases relative to V so that $(1 - V/c)$ becomes smaller in value. Figure 8 illustrates his results together with data from several other observers. To this set of data a good fit is made by the curve

$$\frac{c}{V} = 1 + \frac{3}{4} \frac{t}{V} \quad (19)$$

in which t/V is in sec. Unfortunately, no further similarity analysis can be pursued from this point since the range of

fish size covers only threefold and no specific information on the activity level (at which V was measured) is available. (Note that it is incorrect to apply the velocity-length scaling, such as eq. (15), to the right-hand side of (19) since (15) holds only for the full-active level in swimming of fish of various sizes.)

I. Viscous Resistance

The great difficulties of making direct measurement of the drag a fish must overcome in swimming has forced many researchers to assume that it is comparable to the drag on an equivalent stretched-straight body. Although this assumption leaves considerable room for caution, many attempts have been made to measure the viscous drag of either a mechanical model or a paralyzed fish in steady flow in wind or water tunnels, towing tanks, or water tanks for drop-down tests. Another approach has been to observe the retardation of a fish in glide (for reviews see Gray, 1968; Newman and Wu, 1975; Webb, 1975). Generally speaking, the measured values of the drag coefficient C_D show wide scatter over a range of a few times to tens of times the drag coefficient for turbulent drag on a flat plate at the same Reynolds number. However, there are also reports (Lang and Daybell, 1963; Webb, 1975) indicating that the measured drag is close to that of an equivalent mechanical model predicted by boundary-layer theory. These differences between various results can be attributed to the difficulties in performing such experiments.

In connection with the present study, the detailed analysis of Brett (1963) on the swimming energetics of sockeye salmon (*Oncorhynchus nerka*) and the measured drag of dead fish is especially of value. The drag of an anaesthetically killed fish (of similar size) was measured by Brett in a closed water tunnel equipped with fine-grained screens at both ends of the working section. Figure 9 shows the variation of the dead-drag coefficient, C_{Dd} , replotted from Brett's data, with the Reynolds number. The wetted surface of the fish is determined from the allometric equation (Webb, 1977; table 2 for this species)

$$S = 0.23 \pm 2.14 \text{ cm}^2 \quad (2 \text{ in cm}) \quad (20)$$

A least-square error fit to these drag data gives the result

$$C_{Dd} = 15.4 \text{ } Re^{-0.40} \quad (2.5 \times 10^4 < Re < 2 \times 10^5) \quad (21)$$

Also shown in Fig. 9 are the data points of the power coefficient,

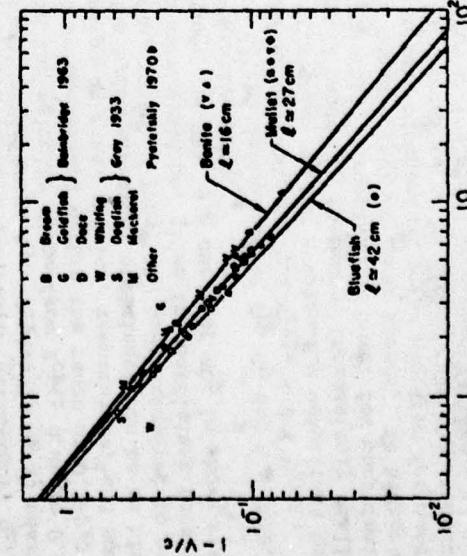


FIG. 8. Variation of $(1 - V/c)$ with the specific swimming speed (V/t) . c denotes the propulsive wave velocity with respect to the body frame of reference.

$$C_p = P / \frac{1}{2} \rho v^3 S \quad (22)$$

based on the measured metabolic rate for swimming, P , of fish of a single size group with mean length $l = 0.178$ m) swimming at various velocities. The curvilinear variation of the C_p with Re ($= Vl/v$, with $v = 0.0114 \text{ cm}^2/\text{s}$ at 15°C) in the log-log plot sharply contrasts with that for C_{pd} of dead fish. C_p first decreases rapidly as the swimming velocity increases from 0.5 ls^{-1} , crossing over the C_{pd} line at $V = 1.3 \text{ ls}^{-1}$ to reach a minimum value of 0.07 (about half the C_{pd} value there) at a velocity 5 ls^{-1} slightly above the critical speed as marked (4 ls^{-1} , $Re = 1.12 \times 10^5$). Beyond the critical speed lies the burst swimming regime in which C_p rises sharply with increasing speed, finally reaching the dead-fish C_{pd} line at a velocity about 8 ls^{-1} , which is nearly the upper limit of performance.

This interesting comparison between C_{pd} and C_p has many implications. First, conversion of swimming metabolic power to the power (DV) required to overcome the swimming drag, D , involves a number of "inefficiencies." They include the loss of heat of reaction in the catabolic processes (conversion of chemical to mechanical power), the increased interior frictional loss and higher power for pumping operations within the circulatory and respiratory systems at higher activity levels, the loss of flow energy associated with vortex shedding, etc. These effects are usually summed in the account of energy budget into two major groups, the muscle efficiency, η_m , and the hydromechanical efficiency, η_h . Typically η_h is nearly constant within the velocity range from V_{crit} down to $0.2 V_{crit}$ and has its value falling within the range of 0.2-0.3 (Webb, 1975) depending on size, species, temperature, and some other factors. The hydromechanical efficiency can be as high as 0.9 or higher (Wu, 1971b). Thus, the power required to overcome the drag in swim would be, given in coefficient form, ηC_p , where $\eta = \eta_m \eta_h$. In Fig. 9 a curve of ηC_p is shown with $\eta = 0.25$ as a representative case.

In view of the variation of C_{pd} , C_p and $\eta = DV/P$, we should then expect that $C_D = \eta C_p$ for $0.2 V_{crit} < V < V_{crit}$. Without adequate modification of the η value for velocities below this range, we would expect C_D to become increasingly smaller than ηC_p due to possible consumption of power for nonswimming purposes (e.g., maneuvering) at lower speeds. At higher burst speeds, the actual biochemical power supplied for muscular activities is recognized to be higher than that measured from the oxygen consumption since an excessive amount is provided at the expense of depletion of energy reserve in the anaerobic muscle. It seems reasonable to expect that the corresponding drag coefficient at these higher frequencies of body undulation would also increase with increasing burst speed similar to the behavior of measured C_p in this speed range. The result of

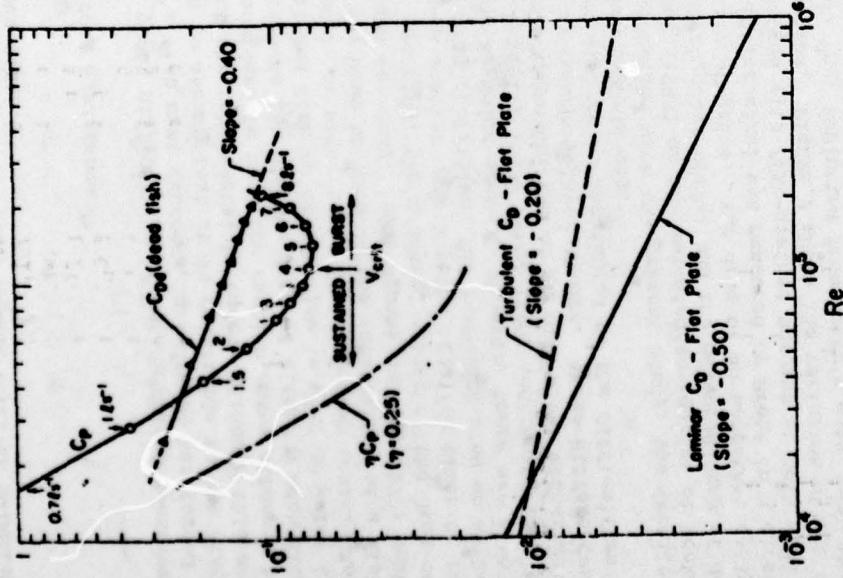


FIG. 9. Variation of the measured metabolic power coefficient, ηC_p , with the Reynolds number and the variation of the measured dead-drag coefficient, C_{pd} , of freshly killed salmon (adapted from Brett, 1963). The corresponding values of the specific speed are indicated in ls^{-1} along the C_p curve. An estimate of the swimming drag coefficient, C_D , is provided by the value of ηC_p shown with a typical value of the overall efficiency $\eta = 0.25$. The drag coefficients of a flat plate for both laminar and turbulent boundary layers are shown for reference.

this analysis thus appears to place C_D considerably below the dead-drag coefficient C_{D0} , and to bring C_D closer to the two reference lines in Fig. 9 for the laminar and turbulent C_D of a smooth flat plate.

The above analysis for the case of a specific size group of fish clears the way for the following comparative physio-mechanical study in which we shall apply again Brett's data (1965a) on P and V for sockeye salmon of five different sizes. When the measured values of P were first plotted versus Re in logarithmic scales, as shown in Fig. 10, we noticed that all the data points lie close to their least-square error mean line:

$$P = (3.55 \times 10^{-11}) Re^{1.88} \quad (\text{watt}) \quad (23)$$

with a small dispersion rather independent of the activity level. Whether there is any intrinsic significance of this activity-independent relationship is not yet clear.

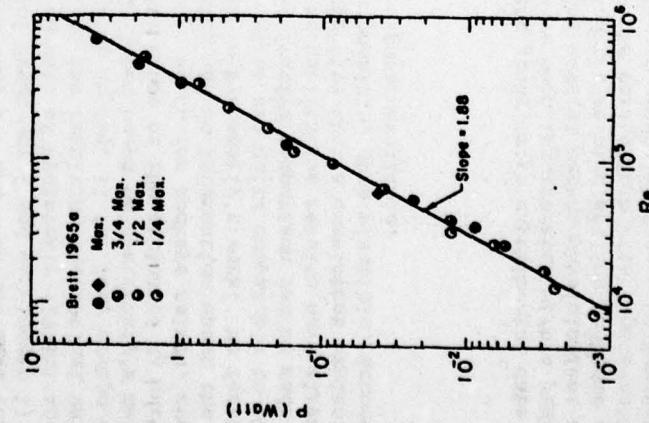


FIG. 10. Variation of the measured metabolic rate for swimming with the Reynolds number for sockeye salmon (adapted from Brett, 1965a).

However, the scale effects are well exhibited in the C_p versus Re relationship as illustrated in Fig. 11, in which the five dashed curves separately connect the four activity levels of each size group. These scale effects could be represented by a least-square error line fitting to the experimental points for each given activity level, but, in view of the appreciable scatter of the data points (which is apparently due to the errors in V being more amplified at higher speeds for C_p by virtue of the definition of C_p), it is thought that the best representation of the result can be obtained by a direct calculation using the already determined mean lines for P and V . The basic allometric equations involved are

$$S = K_S l^\alpha_s \quad (\text{s in m}^2, l \text{ in m}) \quad (24)$$

$$V = K_V l^\alpha_v \quad (\text{v in ms}^{-1}, l \text{ in m}) \quad (25)$$

$$Re = Vl/v \quad (\text{v in m s}^{-1}) \quad (26)$$

$$P = am^b = K_p Re^a \quad (P \text{ in W}) \quad (27)$$

Substitution of these equations in (22) gives

$$C_p = K_{C_p} Re^a C_p \quad (28)$$

$$K_{C_p} = 2 \times 10^{-3} (K_p/K_s) (K_v/v) (a_s^{-3}) / (1 + a_v) \quad (29a)$$

$$a_{C_p} = a_p - 3 - \frac{a_s^{-3}}{1 + a_v} \quad (29b)$$

The computed results based on $K_s = 0.44$, $a_s = 2.14$, eq. (5) and Brett's data are listed in Table III. These regression lines of C_p are shown in solid lines in Fig. 11. At the maximum activity level, the slope of C_p lies between those of the

TABLE III

	b	K_V	a_v	K_p	a_p	K_{C_p}	a_{C_p}
$\frac{1}{4}$ - max	0.889	0.49	0.527	8.4×10^{-11}	1.82	179	-0.617
$\frac{1}{2}$ - max	0.922	0.98	0.525	3.1×10^{-11}	1.89	42	-0.546
$\frac{3}{4}$ - max	0.949	1.47	0.525	1.5×10^{-11}	1.94	17	-0.496
max	0.969	1.96	0.524	6.4×10^{-12}	2.03	6.0	-0.406

laminar and turbulent C_D reference lines. The rate of decrease of C_p with increasing Re becomes more rapid as the activity is reduced to lower levels, implying that larger fish gain more advantage in power saving, relative to smaller fish, at reduced activity levels.

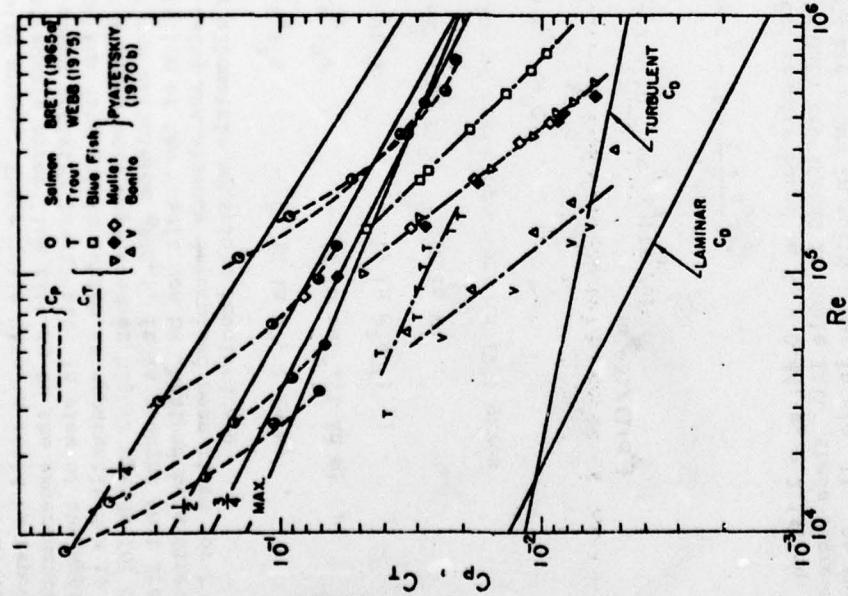
If we further use the overall efficiency η to estimate the propulsive drag coefficient according to $C_D = \eta C_p$, a typical value of $\eta = 0.25$ would place the estimated C_D line at the maximum activity (not shown in Fig. 11) quite close to the turbulent C_D line for a smooth flat plate.

In this connection it is of interest to compare the estimated drag with the theoretically predicted thrust. By slender-body theory (as cited earlier), the mean thrust coefficient has the following approximate expression:

$$C_T = \pi / 2 \rho V^2 S = \frac{\pi}{8} \left(\frac{a_0 b_0}{2} \right)^2 \left(\frac{L^2}{S} \right) \sigma^2 \left(1 - \frac{V^2}{c^2} \right), \quad (30)$$

where a_0 denotes the amplitude of tail beat, b_0 the maximum depth of the caudal fin, $c = w/k = f\lambda$ the wave velocity of the propulsive wave (of frequency f and wavelength λ). By making use of the observed data of Pyatetskiy (1971b) and Webb (1975) on these quantities, the resulting theoretical values of C_T are plotted versus Re in Fig. 11 for four groups of fish. The slopes of these C_T lines based on Pyatetskiy's data are qualitatively similar to those of the estimated C_D curves derived from Brett's results of C_p for sockeye salmon, even though the species do not match and no information about the activity level is available in Pyatetskiy's work. We further note that the predicted C_T values are quite comparable to the estimated C_D , albeit no quantitative comparison can be made at this time. Nevertheless, these qualitative results have already made possible the perspective that a consistent explanation is taking hold for a possible, even plausible, account of the power required and power available.

FIG. 11. Scale effects in the variation of the measured metabolic power coefficient (for swimming) with Reynolds number for five different size groups of sockeye salmon (adapted from Brett, 1965a). Solid lines are least-square error fit to C_p at specific activity levels. Dashed lines show variation of C_p with various activity levels for each size group. Dash-dot lines illustrate theoretical thrust coefficient, C_T , computed from eq. 30 for the data of Pyatetskiy (1970b) and Webb (1975).



J. Conclusion

In the present study, more experimental data on comparative physiology have been incorporated with a previous investigation to discuss several mechanophysiological aspects of fish locomotion and the related scaling problems with particular reference to the carangiform with lunate-tail mode of swimming for different groups of fish. Measurements of metabolic rate at various activity levels, coupled with direct observations of pertinent kinematic parameters such as fish mass, length, swimming velocity, and frequency and wavelength of tail beat, have provided the necessary basis for the present

similarity study. Effects of body size on swimming velocity, specific energy cost, power coefficient, and propulsive wave parameters are found to satisfy specific scaling relationships with the activity level as an intrinsic parameter. These relationships have supplied direct and indirect evidence about the swimming drag coefficient concerning both its functional dependence on the Reynolds number and its order of magnitude. Comparison between the drag coefficient and the power coefficient available for swimming, converted from data on metabolic rate with estimated muscle efficiency and hydromechanical efficiency, indicates their similar dependence on the Reynolds number and their comparable magnitude, which in turn may provide a resolution of Gray's paradox (1936, 1957).

This conference has clarified several essential aspects suggesting that tunas would be the potentially ideal organisms for studying the energetics and ecology of fish. First the scombrids offer a wide range of body sizes for studies of the scale effects. Of further advantage is the salient feature of their continuous swimming at moderate to high sustained speeds which should facilitate measurements of metabolic rate and flow quantities at a more steady level of activity. From the hydrodynamic viewpoint, there are various morphological and physiological features presumably adapted to their high swimming performance (e.g., finlets, slotted dorsal fin, keel peduncle, fairing of their highly streamlined bodies, etc.) which may have great significance yet to be fully understood.

Another striking feature is the "warm body" especially noted for the scombrids. The continuous swimming requirements may explain the relatively high respiration rates estimated by Sharp and Frances (1976) and the high proportions of red aerobic muscle (Rayner and Keenan, 1967, and many contributors to this text). The basic mechanism underlying the heat generation and the need of a heat exchanger in the circulatory system, especially in tropical waters, requires further research for better understanding. It remains to be explored if the selective sites of heat transport, namely those more concentrated along the dorsal and ventral extents of tunas' bodies may have significant effect on the stability of cross flows. It is believed that the difficult problems of the viscous resistance on a swimming fish and the efficiency of the muscle to mechanical energy conversion can also be brought into better understanding by continued collaboration by the physiologist and hydrodynamicist.

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